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Expectations modulate early but not late event-related potential correlates of successful recognition memory

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Expectations modulate early but not late event-related potential correlates of successful recognition memory

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Abstract

Expectations modulate early but not late event-related potential correlates of successful recognition memory

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Recognizing that an item has been previously encountered may not only depend on the strength of memory for that item, but also the expectation that the item will be remembered. Recent studies by O'Connor, et al (2010) and Jaeger et al (2013) revealed that a significant portion of the functional magnetic resonance imaging (fMRI) "retrieval success" effect (BOLD signal for correctly identified old items > new items) depends upon whether participants expect novel or familiar stimuli. The current study examined how expectancy modulates the event-related potential (ERP) retrieval success effect. We employed a typical recognition memory task with the addition of explicit cues indicating if upcoming memory probes were "likely old", "likely new" (with 75% validity), or "unknown". An electrophysiological response to the cue, primarily across frontal electrodes from 700-850ms after cue onset, predicted individual differences in cue-induced bias in memory judgments. Responses to memory probes were examined 300-400ms and 500-700ms after probe onset, corresponding to time windows previously associated with ERP correlates of memory processing. Differences between old and new

items were greatest from 300-400ms when preceded by “likely old” cues, overlapping with a component previously identified as tracking familiarity-based processing. In contrast, the 500-700ms time window, previously associated with recollection, revealed significant differences between old and new items that were not modulated by cue type. Overall this pattern of results shows that cue induced biases influence earlier (300-400ms after onset of a memory probe) but not later retrieval processing (500-700ms).

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Chapter 1: Background and Specific Aims

1.1 Parietal cortex and the "retrieval success" effect

The introduction of human brain imaging techniques precipitated decades of research seeking neural correlates of memory processing. One of the most reliable findings comes from recognition memory studies using event-related brain potentials (ERP; the average brain electrical activity elicited by a specific event) in which correctly identified old items elicit greater amplitude signals than correctly identified new items. This is known as an "old-new" or "retrieval success" effect. Some prior ERP studies reveal two distinct retrieval success effects; one maximal over frontal scalp areas with onset approximately 300ms post stimulus, and another maximal over left parietal scalp areas with onset 400ms or later post stimulus (for overviews see Friedman & Johnson, 2000; Rugg & Allan, 1995; Rugg & Curran, 2007). The earlier effect has been found in ERPs even when participants cannot correctly report unique contextual details about the item or only report a "feeling" that the item is old (Curran, 2000; Düzel, Yonelinas, Mangun, Heinze, & Tulving, 1997). The memory process thought to underlie this component is termed familiarity – a process that discriminates old from new items on a general sense of a prior encounter rather than reference to the unique encoding episode. In contrast, the later left parietal effect reliably tracks the depth of encoding and the quality of source memory retrieval (Rugg & Curran, 2007; Vilberg & Rugg, 2009; Vilberg, Moosavi, & Rugg, 2006), so researchers have argued that it likely reflects processes directly associated with recollection.

More recent studies using functional magnetic resonance imaging (fMRI) have also revealed retrieval success effects in parietal regions, where greater activity is seen when contrasting correctly identified old items with correctly rejected new items

(Wagner, Shannon, Kahn, & Buckner, 2005). Since the distribution of the retrieval success effect in ERPs over left parietal scalp areas is largely consistent with generation in parietal cortex, some researchers assume the fMRI and ERP recollection effects are analogous (Rugg & Curran, 2007; Vilberg & Rugg, 2009), and recent evidence combining MEG and fMRI further suggests that these effects share common generators in posterior parietal cortex (PPC) (Bergström, Henson, Taylor, & Simons, 2013). Activations in PPC, particularly the angular gyrus and supramarginal gyrus, scale with the amount or quality of episodic detail recalled, linking these regions to recollection (Daselaar, Fleck, & Cabeza, 2006; Henson, Hornberger, & Rugg, 2005; Montaldi, Spencer, Roberts, & Mayes, 2006; Vilberg & Rugg, 2007; 2009). However, activations in neighboring superior regions of PPC, particularly the intraparietal sulcus, have been repeatedly observed when subjects correctly recognize an item without source memory, leading researchers to link these activations with familiarity, rather than recollection (Daselaar et al., 2006; Henson et al., 2005; Montaldi et al., 2006; Yonelinas, Otten, Shaw, & Rugg, 2005).

Interpretations of the ERP and fMRI retrieval success effects focus on the potential role of the parietal lobe in recognition memory. A number of possible theoretical frameworks have been presented, including the view that parietal cortex may buffer retrieved episodic content (Wagner et al., 2005; Yu, Johnson, & Rugg, 2012), or that it is involved in orienting other regions to the contents of memory, (Rugg, Otten, & Henson, 2002; Wagner et al., 2005) or that it accumulates evidence from other retrieval processing areas to produce a signal of perceived oldness (Wagner et al., 2005; Wheeler & Buckner, 2003).

However, considerable functional heterogeneity among parietal sub regions has been documented using fMRI. For instance, while parts of the ventral PPC may be

closely linked to the maintenance of episodic content in some studies (Yu et al., 2012) other parietal regions have been implicated in a variety of other retrieval roles. Other memory task designs yield additional PPC activations not directly linked to recollection, but rather linked to memory orienting. Dobbins and colleagues found that parietal regions including the inferior parietal lobule were associated with selective attention to a particular class of episodic details rather than retrieval success (Dobbins, Rice, Wagner, & Schacter, 2003) and more recently, Ciaramelli and colleagues found regions of dorsal parietal cortex associated with top-down orienting of memory based on explicit cues (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010). Overall, these results suggest roles for parietal cortex beyond "retrieval success" - while parietal cortex is reliably activated during memory retrieval and so perhaps plays a critical role in that process, the role may not be constrained to processes downstream from episodic retrieval.

Despite the reliable engagement of parietal cortex in memory retrieval, the memory performance of patients with parietal lobe lesions raises questions about whether these regions are necessary for successful recollection. Patients with parietal lesions often exhibit no appreciable accuracy impairment on tests of recognition memory, and may even display intact source recollection, albeit with somewhat reduced confidence in their memory decisions (Berryhill, Drowos, & Olson, 2009; Simons et al., 2008; Simons, Peers, Mazuz, Berryhill, & Olson, 2010). If the parietal lobes do not serve a function directly necessary for successful recollection, then what do functional correlates of successful memory retrieval reflect?

1.2 EXPECTATIONS INFLUENCE NEURAL CORRELATES OF RECOGNITION

Attempting to address the conflicting evidence from lesion and imaging studies, O'Connor and colleagues (O'Connor, Han, & Dobbins, 2010) and Jaeger and colleagues (Jaeger, Konkel, & Dobbins, 2013) tested the role that expectancy plays in the parietal retrieval success effect. Drawing on analogies between visual and mnemonic orienting (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008) they predicted that some activations in lateral parietal cortex may track the orienting of attention following unexpected memory signals, rather than the retrieval of episodic content itself. They collected fMRI data while employing a study-test recognition task, with the addition of explicit cues preceding test items to manipulate subjects' mnemonic orientation independently of the memory probe (similar to the Posner visual cueing task used to study spatial orienting (Posner, Snyder, & Davidson, 1980)). Cues indicated if the upcoming word was "likely old" or "likely new" and were 75-80% accurate. Both studies found that the angular gyrus, a lateral inferior parietal area previously associated with recollection (Daselaar et al., 2006; J. D. Johnson & Rugg, 2007; Spaniol et al., 2009; Vilberg & Rugg, 2009) was sensitive to cueing, and in addition, Jaeger and colleagues found other areas of left lateral PPC where activations depended upon whether or not memory items were consistent with expectations. Activations in the angular gyrus were greater for old items, but only when they were unexpected, while in other areas such as the anterior intraparietal sulcus (IPS), activation was greatest for new items, but only when they were unexpected, while other mid-IPS regions showed greater activation on all trials in which memory probes violated expectations, whether they were old or new. These findings do not align well with previous formulations of the parietal retrieval success effect as directly supporting recollection, since elevated responses to unexpected novelty were present despite the lack of episodic detail for those items. They note that some observed PPC expectancy effects

must be contingent on a rapid initial assessment of memory for an item, without reference to unique episodic details. They conclude that the left PPC signal does not reflect the level of familiarity alone, but rather a process downstream, reflecting both the level of familiarity and its salience or relevance in the current context, which may be important for reorienting of attention or further effortful attempts at recollection.

The alternative explanation of the fMRI retrieval success effect proposed by these studies may also apply to the corresponding ERP effect. Electrophysiological evidence from other cognitive domains already suggests that multiple ERP components may be influenced by expectations about experimental stimuli. For instance, in some perceptual discrimination tasks, a positive component with a similar central parietal topography and latency as the retrieval success effect, termed the P3b, has been found to index improbable task-relevant stimuli (for reviews see (Polich, 2007; Soltani & Knight, 2000). Another component called the P600 has been found to index semantic incongruences (Coulson, King, & Kutas, 1998; Osterhout & Holcomb, 1992). These findings from other domains have lead some memory researchers to suggest that the amplitude of the retrieval success effect in ERPs may also be influenced by the high relevance and low probability of an item correctly identified as old in a memory task (Neville, Kutas, Chensney, & Schmidt, 1986; K. M. Spencer, Abad, & Donchin, 2000). Herron and colleagues (Herron, Quayle, & Rugg, 2003) tested this explicitly by manipulating the ratios of old to new items in a recognition task and found no effect on the typical retrieval success ERP component at a latency of 500-800ms, but a medial parietal component seen after 800ms varied in amplitude with the probability of the probes. While they note that the topography and time course of this probability effect makes it dissociable from the retrieval success effect in their design, they note that in other cases mnemonic and non-mnemonic factors (such as expectation) may be less separable. In light of these studies, it

seems probable that processes other than successful recollection may contribute in significant ways to ERP correlates of memory.

1.3 Specific aims

The purpose of the current study is to examine the effects of expectancy on the ERP retrieval success effect using a cueing paradigm similar to O'Connor and colleagues. Given the low temporal resolution of fMRI, there is reason to believe that the ERP may reveal additional information about the relationship between cue effects and retrieval success effects. If a left parietal expectation-sensitive component is found which temporally precedes or overlaps the recollection component, this may also be consistent with the view that the role of PPC is not constrained to downstream processing supporting recollection. By contrast, if a late positive parietal component is insensitive to cueing and only modulates with the actual memory status of a probe, this would further support prior work indicating that the left parietal component tracks recollection. In addition, the precise temporal resolution will allow examination of the electrophysiological response to the cues, which should correspond to behavioral shifts in response bias to the memory probes.

Chapter 2: Methods

2.1 Participants

Complete data was collected from 31 right-handed native English speakers with no diagnosis of a psychological or neurological disorder. Data from three participants was not useable due to technical recording problems, and data from an additional four participants was discarded due to failure to complete the task as instructed (a low raw accuracy score – proportion of hits minus false alarms below .25) or severe recording artifacts, leaving data from 24 participants for final analysis (12 female, mean age 20.9 years). All participants signed informed consent as required by the Institutional Review Board at the University of Texas at Austin.

2.2 Experimental Task

Participants engaged in a cued recognition memory task using word stimuli while we recorded 71 channels of EEG. Four hundred words were randomly selected for each participant from a single source list of 1216 words originally used by O'Connor and colleagues (O'Connor et al., 2010). Words had a mean of 7.08 letters and a mean Kucera-Francis frequency of 9.33. Each participant completed a total of four study-test block pairs. Following a brief training block with feedback, participants began the experimental trials, in which no performance feedback was given. A sample study-test sequence is shown in Figure 1.

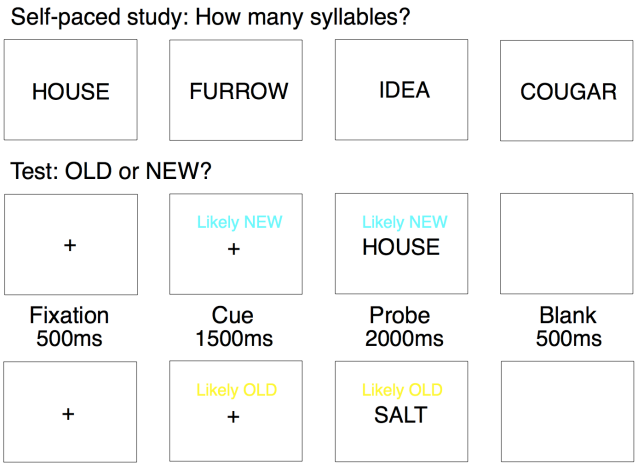

Figure 1: Sample task sequence

Beginning with a study block, participants studied 50 words at their own pace by indicating the number of syllables in a displayed word. Immediately following each study block, participants completed a test block with 100 words, including 50 words previously studied and 50 new words, presented in random order. EEG was recorded continuously during the test phases. Each test trial began with a fixation cross that appeared on the screen for 500ms. This was followed by a cue presented above the fixation cross indicating if the upcoming word would be "likely old" (in yellow font, 40% of trials), "likely new" (in blue font, 40% of trials) or "unknown" (in white font, 20% of trials). See condition abbreviations in Table 1 below. The cue remained on the screen for 1500ms, then the fixation cross below the cue was replaced by a centrally located probe word for two seconds. Cues remained on screen during this two-second response window. During presentation of the probe word, participants indicated with a button press if the probe word was previously studied or new. Responses were followed by 500ms blank screen before the fixation cross for the next trial appeared. Participants were instructed to respond as quickly as possible without sacrificing accuracy. Cues were highly likely

(75%) to correctly predict the status of the probe word, and participants were explicitly informed of this probability.

	Correctly Identified OLD	Correctly Identified NEW
Cue "Likely Old"	LO hit (valid trial)	LO CR (invalid trial)
Cue "Likely New"	LN hit (invalid trial)	LN CR (valid trial)
Cue "Unknown"	UN hit (neutral trial)	UN CR (neutral trial)

Table 1: Abbreviations of experimental conditions.

2.3 EEG RECORDING AND ANALYSIS

Continuous EEG data was recorded during the task using a 71-channel Biosemi system, with 64 active electrodes embedded in a mesh cap using the standard and extended international 10-20 electrode locations, five freestanding ocular electrodes, and two mastoid reference electrodes. Lateral and vertical occular movement was recorded from freestanding electrodes on the left and right canthus and below the left and right pupil. Data were recorded using the Biosemi Active II amplifier in 24 bit DC mode sampling at 256 Hz. Recordings were referenced to a common mode sense active electrode during the task. Active electrodes do not require skin preparation to reduce impedance, but half-cell potentials of the interface between the skin, gel and electrodes were kept below ±40mV, in line with manufacturer recommendations.

Data were imported and processed using the EEGLab toolbox version 11.0.3.3b for the MATLAB environment (Delorme & Makeig, 2004). First, data were re-referenced to linked bilateral mastoid electrodes and divided into epochs encompassing an entire trial, which included the complete fixation, cue and memory probe interval (4.5s total). Artifacts were removed with a combination of visual assessment (such as severe EMG artifact and amplifier saturation) and EEGlab functions that detected trials with abnormal

values (>25uV or <-25uV), abnormal spectra (>50Hz), abnormal slope (>50 uV/epoch) or abnormally large amplitudes (values greater than 5 standard deviations from a channel mean). After artifact rejection, bad channels were interpolated using the EEGlab spherical spline function (no more than 2 channels interpolated for any subject) and trials containing only minimal ocular artifact were corrected using an adaptive filter-based regression (He, Wilson, & Russell, 2004). Epochs were then highpass filtered at .01Hz, and lowpass filtered at 20Hz. The cue interval and probe intervals were then separated and baselined to the preceding 200ms before cue and probe onset, respectively, and examined separately.

2.3.1 Cue Period

We first examined the interval from 0ms to 1500ms after cue onset (the full duration of the interval when only the cue was displayed) with a baseline of 200ms prior to cue onset, during the fixation interval. Epochs were sorted into 3 conditions based on the cue type - "likely old" (LO), "likely new" (LN) and "unknown" (UN) and cue interval ERPs were generated for each condition for each subject. ERP components to be analyzed were selected through visual inspection of topographic maps.

2.3.2 Probe Period

For the probe period analysis, we examined the interval from 1500ms (the onset of the probe) to 3500ms (the end of the response window) with a baseline from 1300ms to 1500ms (end of cue interval). Epochs were sorted into the six conditions shown in Table 1, and one average was created for each unique combination of cue type and probe type. ERP components for analysis were identified from inspection of the grand average waveforms and topographic maps.

Chapter 3: Results

Data were exported and statistically analyzed in R for Mac OS X version 2.14.2. (R Development Core Team, 2012). Parametric analysis of variance tests are reported with Greenhouse-Geisser (GG) correction where applicable, and all t-tests conducted are reported with Holm correction for multiple comparisons where applicable.

3.1 Behavioral results

Reaction times for trials with a correct response only were examined using within-subjects repeated measures ANOVA, with factors for cue type (LO/LN/UN) and response outcome (hit/CR). A significant main effect of response outcomes was found ($F(1,23) = 12.70$, $p = 0.002$), as well as a significant interaction of cue type and response outcome ($F(2,46) = 7.55$, $p[GG] = 0.002$). Hits were significantly faster than correct rejections overall, and this effect was significant when comparing hits and CRs on "likely old" ($p = 0.006$) or neutral trials ($p = 0.033$), but not "likely new" trials ($p = 0.566$). Mean reactions times for each condition are shown in Table 2 below.

	Old Probe	New Probe
Cue "Likely Old"	894 ms	975 ms
Cue "Likely New"	929 ms	948 ms
Cue "Unknown"	904 ms	966 ms

Table 2: Mean reaction times by cue condition

Accuracy was examined by calculating d' (the normed proportion of correctly identified old items to items incorrectly identified as old) and bias (C, the tendency to respond old or new), to determine how cueing affected behavioral responses. Each was examined separately using within subjects repeated measures ANOVA with factors for

each cue type (LO/LN/UN). The analysis of d' scores revealed no significant effect of cue type ($F(2,46)=0.34$, $p[GG]=0.714$), showing that subjects were equally accurate regardless of cued expectations. However, bias scores revealed a significant main effect of cue type ($F(2,46)=6.171$, $p[GG]=0.005$). Bias scores revealed that subjects were reliably more liberal with old responses following the "likely old" cues compared to the neutral cues, ($p=0.007$) and they were more liberal with old responses following the neutral cues than the "likely new" cues ($p=0.011$). These results show that subjects shift their response bias in accordance with cues, indicating subjects used cues as expected to inform their responses. Accuracy and bias are shown in Figure 2 below.

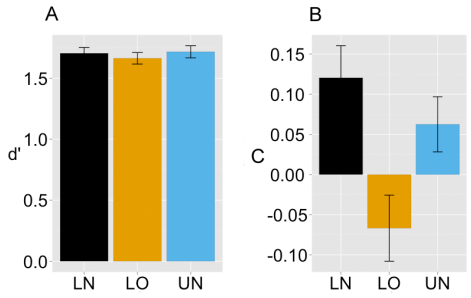

Figure 2: A) Accuracy scores and B) bias scores, by cue condition.

3.2 ERP Results

3.2.1 Cue Period

Three groupings of electrodes were chosen for analysis based on inspection of topographic maps. Electrode groupings are as shown on the left in Figure 3; a frontal group consisting of the average of Fp1/AF7/AF3 on the left and Fp2/AF8/AF4 on the right, a central group consisting of the average of FC1/FC3/C1/C3 on the left and FC2/FC4/C2/C4 on the right, and a parietal-occipital group consisting of P1/P3/PO3 on the left and P2/P4/PO4 on the right.

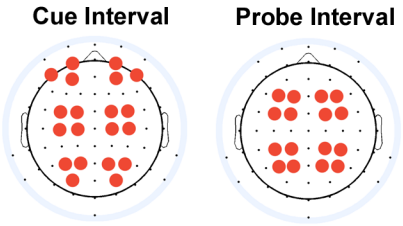

Figure 3: Electrode montage chosen for cue and probe interval analysis

We noted two components of primary interest in the cue interval; a negativity prominent over central and posterior scalp from 300-400ms after cue onset, and a slow positivity prominent over frontal and central scalp maximal around 700-850ms after cue onset. Mean amplitude values from each time range were examined with repeated measures ANOVA, with factors for cue type (LO/LN/UN), location (frontal, central and parietal), and hemisphere (left and right). For the 300-400ms range, significant main effects of cue ($F(2, 46) = 5.23$, $p[GG] = 0.021$) and location ($F(2, 46) = 11.10$, $p[GG] = 0.002$) were found, with no interactions. Amplitudes elicited by neutral cues were significantly more negative than "likely old" cues ($p=0.031$), and "likely new" cues ($p=.022$), but "likely old" and "likely new" cues were not significantly different ($p = .742$). Amplitude differences by cue type were most evident at central scalp sites in this time range.

For the 700-850ms range, significant main effects of cue ($F(2, 46) = 4.01$, $p[GG] = 0.034$) and location ($F(2, 46) = 4.75$, $p[GG] = 0.026$) were found, with no interactions. Amplitudes to "likely old" cues were significantly more positive than "likely new" cues ($p=0.005$), but neither "likely old" nor "likely new" cues were significantly different from neutral cues ($p=0.102$ and $p=0.666$, respectively). Although the interaction of cue and location was not significant, the largest average differences between "likely old" and

"likely new" cues were seen at bilateral prefrontal and left central scalp sites, as shown in the topographic map in Figure 4.

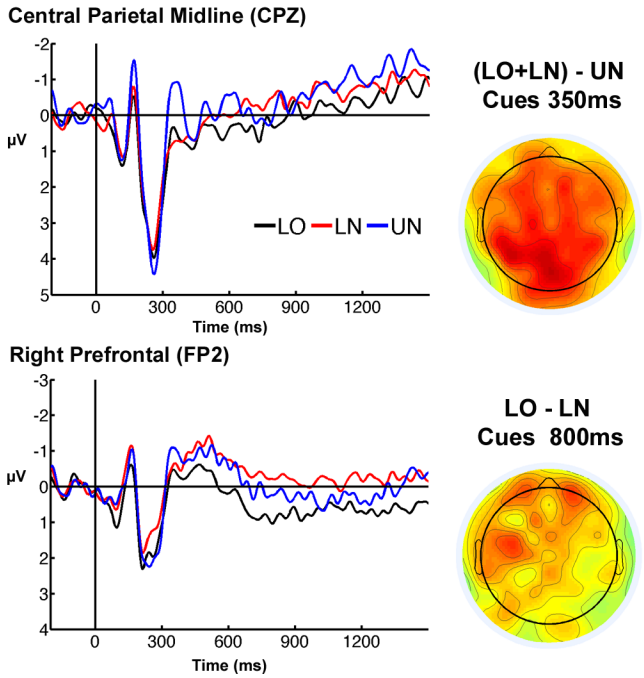

Figure 4: Cue interval ERPs and topographic maps at two representative electrode sites, one right prefrontal (FP2) and one central-parietal (CPZ). Time zero represents cue onset, baselined to preceding fixation interval.

In order to determine the relationship between the electrophysiological cue response and subsequent behavioral shifts in recognition bias, we examined correlations between mean amplitude for each time range at the two groups of bilateral prefrontal sites that showed large cue effects (AF3/FP1/AF7 and AF4/FP2/AF8) and response bias (C). Across both the 300-400ms time range and the 700-850ms range, more positive amplitude at frontal sites in response to cues was generally associated with subsequently more conservative responses (more likely to respond "new"), regardless of the cue type. For example, during the 300-400ms interval, significant positive correlations were found between amplitude at left frontal sites in response to the "likely old" cues and the

subsequent behavioral decision bias for probe recognition judgments in this condition ($r = 0.53$, $p = 0.008$). An analogous relation was observed during "likely new" ($r = 0.49$, $p = 0.015$) and neutral cue trials ($r = 0.59$, $p = 0.002$) such that the ERP cue response positively correlated with the subsequent behavioral decision bias. The left frontal response to "likely new" cues showed a similar non-specific pattern of correlation; amplitude on those trials was significantly positively correlated with bias for "likely old" ($r = 0.43$, $p = 0.037$) and neutral trials ($r = 0.44$, $p = 0.030$).

300-400ms	LO right frontal	LO left frontal	LN right frontal	LN left frontal	UN right frontal	UN left frontal
Bias LO	0.53*	0.49*	0.50*	0.43*	0.17	0.23
Bias LN	0.37	0.49*	0.32	0.37	0.17	0.27
Bias UN	0.52*	0.59*	0.44*	0.44*	0.08	0.18

Table 3: Correlations between amplitude at frontal sites from 300-400ms after cue onset, and the behavioral measure of response bias, C. Starred values indicate $p>0.05$

Amplitude for "likely old" trials at the same sites during the later interval, 700-850ms, was also positively correlated with bias for "likely old" ($r = 0.52$, $p = 0.009$) as well as "likely new" trials ($r = 0.46$, $p = 0.023$).

700-850ms	LO right frontal	LO left frontal	LN right frontal	LN left frontal	UN right frontal	UN left frontal
Bias LO	0.51*	0.52*	0.31	0.06	0.20	0.28
Bias LN	0.31	0.46*	0.07	0.12	0.02	0.04
Bias UN	0.32	0.29	0.23	0.11	-0.18	-0.08

Table 4: Correlations between amplitude at frontal sites from 700-850ms after cue onset, and the behavioral measure of response bias, C. Starred values indicate $p>0.05$

Overall this pattern suggests that the frontal ERP response to cues, regardless of their forecast, anticipates a conservative response style. O'Connor et al. (2010) found that during uncued, standard recognition, lateral parietal responses for hits and correct rejections reliably tracked individual differences in overall decision bias and not accuracy, demonstrating that the processing of probes was influenced by the general decision biases of the subjects. Other studies have indicated that such list-wide decision biases may be relatively stable for each participant (Aminoff et al., 2012). Given this, we reasoned that the manner in which the anticipatory cues were processed might differ as a function of each subject's measured bias during neutral trials. For example, a generally strict participant may respond to a cue signaling "likely old" because such a cue conflicts with his or her general tendency to respond "new" when shown a neutral cue. To address this, we median split the group depending upon the measured bias during neutral recognition trials. The median value of bias for neutral cue trials was used to assign participants to a strict ($C > 0.18$) or lax ($C < 0.18$) group. ANOVA was performed for each time range as before, with within-subjects factors for cue type (LO/LN/UN), location (frontal, central and parietal), and hemisphere (left and right) and an additional between-subjects factor for response strategy (strict/lax). The significant main effect of cue type found previously for the 300-400ms time range was preserved ($F(2, 44) = 13.51$, $p[GG] = 0.020$), while the response strategy factor did not significantly predict amplitude for the 300-400ms component ($F(1, 22) = 1.49$, $p = 0.235$), nor were there any significant interactions with cue type and response strategy ($F(2, 44) = 1.29$, $p = 0.279$). However, there was a significant interaction of response strategy and cue type for the 700-850ms component ($F(2, 44) = 1.29$, $p[GG] = 0.032$). Strict responders showed significant amplitude differences by cue type at frontal sites (LO vs LN $p = 0.008$ and LO vs UN p

= 0.001) while lax responders did not show any significant differences by cue type, although "likely new" cues were marginally different from "likely old" and neutral cues (LO vs LN p = 0.052, UN vs LN p = 0.052), as shown below in Figure 5. These data suggest that the processing of the anticipatory cues is influenced by the decision style or strategy of the participant – changes in amplitude during the late cue interval are seen for the cue type which contradicts a participant's default response tendency.

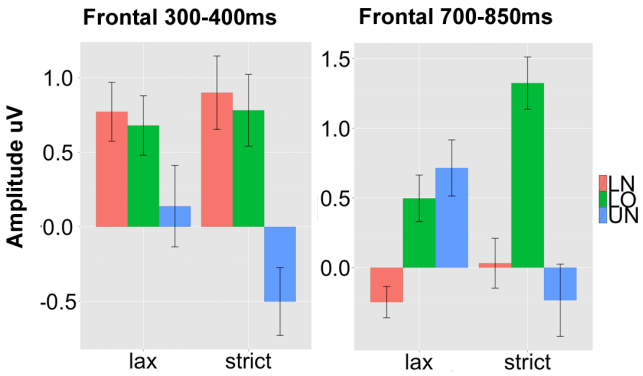

Figure 5: Bar plots of mean amplitude from 300-400ms and 700-850ms after cue onset, averaged over left and right frontal electrode groups, by response bias group. "Strict" indicates a score above the median value of response bias (more likely to respond new), while "lax" indicates a score below the median.

3.2.2 Probe Period

Visual inspection of the ERPs collapsed across cue type indicated the presence of the expected old-new effects (components showing amplitude for hits > amplitude for CRs) in the periods from 300-400ms and 500-700ms, shown in Figure 6.

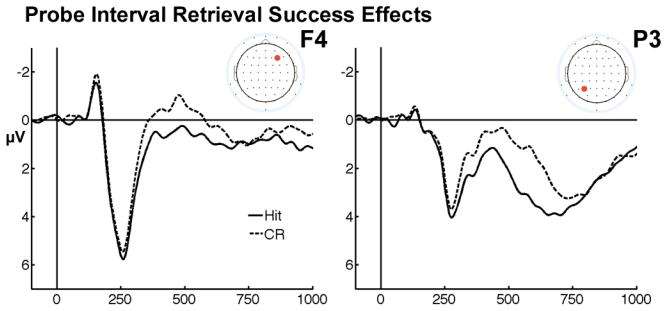

Figure 6: Retrieval success effects collapsed across cue type at two representative electrode sites – right frontal (F4) and left parietal (P3).

Four electrode groupings were chosen based on topographic maps of hit>CR effects and prior literature indicating the typical distribution of these effects (for review see Rugg & Curran, 2007) - clusters covering left frontal scalp (F1/F3/FC1/FC3), right frontal scalp (F2/F4/FC2/FC4), left parietal scalp (CP1/CP3/P1/P3) and right parietal scalp (CP2/CP4/P2/P4). Refer to Figure 3 for illustration of this electrode montage. The 300-400ms and 500-700ms components overlapped topographically, with the later component maximal at left parietal electrodes and the earlier component maximal at both frontal and parietal electrodes. For each component, we compared retrieval success effects under each cue type; the neutral cue conditions (UN hits and UN CRs) were compared first to the "likely old" conditions (LO hits and LO CRs) and then to the "likely new" conditions (LN hits and LN CRs) with repeated measures ANOVA. Subsequent tests separately compared hits of all cue types, and correct rejections of all cue types, to further determine if expectation effects manifested when subjects encountered unexpected novelty or unexpected familiarity, or both. Importantly, this analysis shows if expectation-driven effects are generally earlier or later, relative to the classic retrieval success effects when no clear expectation is established pre-retrieval.

3.2.1.1 Early Probe Period 300-400ms

Expectation effects in the time range from 300-400ms after memory probe onset were tested, first comparing "likely old" to neutral cue conditions using repeated measures ANOVA, with factors for cue type (LO/UN), response (hit/CR), and location (left frontal/ right frontal/ left parietal/ right parietal). A main effect of response was found ($F(1,23) = 8.48$, $p = 0.008$), as well as a significant main effect of location ($F(3,69) = 20.65$, $p[GG] \sim 0.000$), and a significant two-way interaction of cue type and response ($F(1,23) = 4.70$, $p[GG] = 0.040$). Inspection of topographic maps shown in Figure 7 revealed differences between hits and correct rejections across a wide scalp area for the "likely old" condition, but particularly the left and right frontal and left parietal scalp, while no area showed a large hit/CR effect for neutral cues.

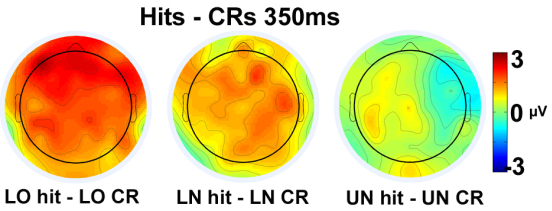

Figure 7: Topographic maps of mean amplitude for hits minus amplitude for correct rejections at 350ms after memory probe onset, by cue condition

The interaction of cue type and hit/CR was further tested with Holm-corrected pairwise tests of amplitude at these sites. The retrieval success effect was significant for "likely old" cues (amplitude for LO hits > LO CRs, $p = 0.001$ at left frontal sites, $p = 0.010$ at right frontal sites, $p \sim 0.000$ at left parietal sites). However, retrieval success effects were absent at all locations for neutral cues (amplitude for UN hits > UN CRs, $p = 0.396$ at left frontal sites, $p = 0.999$ at right frontal sites, $p = 0.571$ at left parietal sites, see Figure 8).

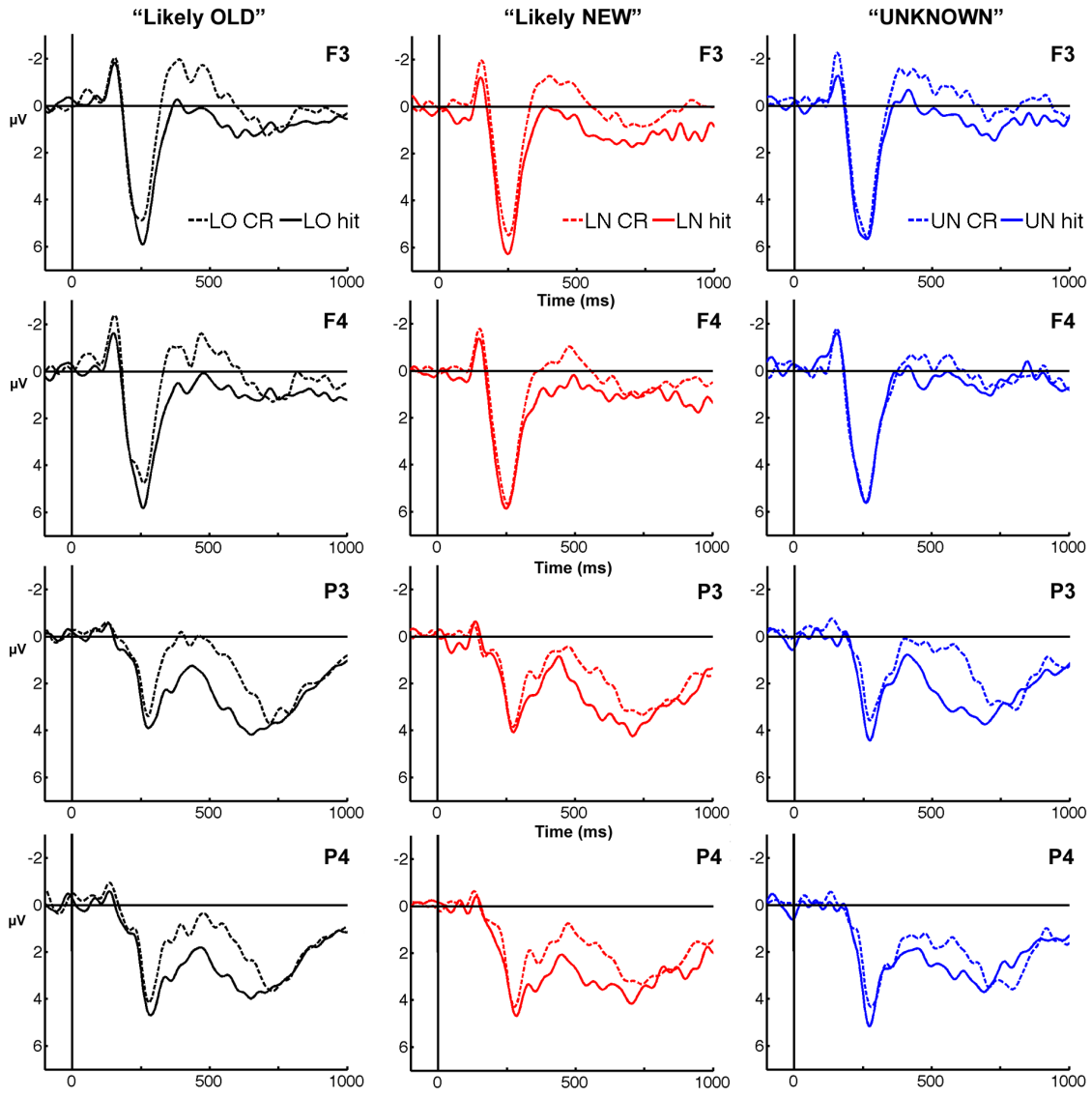

Figure 8: Plots of event-related potentials by cue condition at left frontal (F3), right frontal (F4), left parietal (P3) and right parietal (P4) electrode sites.

"Likely new" trials were also compared to neutral cue trials using repeated measures ANOVA with the same factors. A significant main effect of hit/CR was found ($F(1,23) = 5.45$, $p = 0.028$) as well as a significant main effect of location ($F(3,69) = 22.97$, $p[GG] \sim 0.00$). No significant main effects of cue type, nor significant interactions

with cue type were found. Inspection of topographic maps shown in Figure 7 revealed that the retrieval success effect was greatest at right frontal sites under the "likely new" condition. Holm-corrected pairwise tests revealed that this effect was marginal for the "likely new" cue condition (amplitude for LN hits > LN CRs, $p = 0.072$ at right frontal sites), and again, absent for the neutral condition (UN hits > UN CRs $p = 0.999$ at right frontal sites).

Overall this pattern shows that mnemonic expectations contribute to retrieval success effects seen in this time range; when a participant is oriented to novelty or when the cue does not provide a clear memory orientation, this component does not reliably discriminate old and new items, but when the participant is oriented to familiarity, a large retrieval success effect is seen at both frontal and parietal sites.

Having verified that expectations modulate this early retrieval component, we also wished to examine if it was modulated more by unexpected familiarity, or unexpected novelty. Amplitude data for each hit type (LO hit/LN hit/UN hit) was compared for only the locations that showed significant retrieval success effects in the previous analysis, separately for each location, using Holm-corrected pairwise tests. At all sites, amplitude for all hits was statistically equivalent regardless of cue type (LN hit vs LO hit $p = 0.92$ at left parietal sites, $p = 0.97$ at right frontal sites, and $p = 0.99$ at left frontal sites, and LN hit vs UN hit $p = 0.92$ at left parietal sites, $p = 0.83$ at right frontal sites, and $p = 0.99$ at left frontal sites). However, amplitude for correct rejections did vary by cue type – "likely old" CRs elicited significantly more negative potentials than "likely new" CRs at left parietal sites ($p = 0.035$) and this contrast was also borderline at left frontal sites ($p = 0.063$) and right frontal sites ($p = 0.100$). However, "likely old" CRs were not significantly more negative than neutral CRs at any location (LN CR vs UN CR

p = 0.380 at left parietal sites, p = 0.100 at right frontal sites, and p = 0.197 at left frontal sites).

Overall these tests show that expectation does modulate retrieval success effects during the period from 300 to 400ms after the presentation of a memory probe. Amplitude for correct rejections was generally lower than hits, but this difference was significant for trials with "likely old" cues, but did not reach significance when cues were "likely new" or neutral. Expectations effects were seen predominantly when new items were unexpected. Amplitude was more negative for trials with a "likely old" cue followed by a correct rejection than a "likely new" cue followed by a correct rejections, while amplitude was statistically equivalent for hits regardless of cue.

3.2.1.2 Late Probe Period 500-700ms

Retrieval success effects were again compared for "likely old" and neutral cues 500-700ms after memory probe onset, in the same manner as the previous analysis. A significant main effect of hit/CR was found ($F(1,23) = 16.23$, $p \sim 0.000$), as well as a significant main effect of location ($F(3,69) = 38.84$, $p[GG] \sim 0.000$) and a significant interaction of hit/CR and location ($F(3,69) = 8.42$, $p[GG] = 0.001$). Inspection of topographic maps shown in Figure 9 revealed large differences between hits and correct rejections at left parietal scalp for both the "likely old" and neutral conditions.

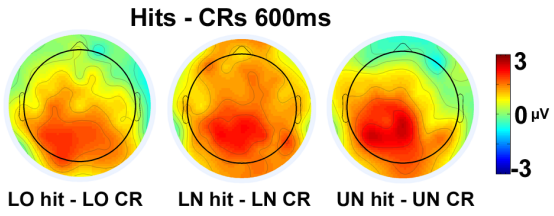

Figure 9: Topographic maps of mean amplitude for hits minus amplitude for correct rejections at 600ms after memory probe onset, by cue condition

The interaction of location and hit/CR was further tested with Holm-corrected pairwise tests of amplitude at all sites. The retrieval success effect was significant for "likely old" cues (amplitude for LO hits > LO CRs, $p = 0.040$ at left frontal sites, $p = 0.041$ at right frontal sites, $p \sim 0.000$ at both left and right parietal sites). Retrieval success effects were also significant at parietal sites, but not frontal sites for neutral cues (amplitude for UN hits > UN CRs, $p = 0.116$ at left frontal sites, $p = 0.382$ at right frontal sites, $p = 0.002$ at left parietal sites, and $p = 0.045$ at right parietal sites).

"Likely new" trials were also compared to neutral cue trials using repeated measures ANOVA with the same factors. A significant main effect of hit/CR was found ($F(1,23) = 10.81$, $p = 0.003$) as well as a significant main effect of location ($F(3,69) = 36.98$, $p[GG] \sim 0.00$), and a significant interaction of hit/CR and location ($F(3,69) = 6.01$, $p[GG] = 0.004$). Inspection of topographic maps shown in Figure 9 revealed that the retrieval success effect was greatest at left parietal sites for "likely new" cues. Holm-corrected pairwise tests revealed that this effect was significant for the "likely new" cue condition only at left parietal sites (amplitude for LN hits > LN CRs, $p = 0.090$ at left frontal sites, $p = 0.360$ at left frontal sites, $p = 0.042$ at left parietal sites, and $p = 0.072$ at right parietal sites), and again, also significant for the neutral condition at left parietal sites (amplitude for UN hits > UN CRs, $p = 0.116$ at left frontal sites, $p = 0.500$ at right frontal sites, $p = 0.003$ at left parietal sites, and $p = 0.072$ at right parietal sites).

The overall pattern of results at left parietal sites confirms that this component is primarily sensitive to an item's status in memory. Having verified that expectations do not appear to modulate this later retrieval component, we sought to further confirm that amplitude for hits and correct rejections did not vary by cue type at left parietal sites. Amplitude data for each hit type (LO hit/LN hit/UN hit) was compared for only left

parietal sites, using Holm-corrected pairwise tests. Amplitude for all hits was statistically equivalent regardless of cue type (LN hit vs LO hit p = 0.95 at left parietal sites, and LN hit vs UN hit p = 0.99 at left parietal sites). Repeating this test for correct rejections, we found that amplitude for correct rejections also did not vary by cue type in this time range (LN CR vs LO CR p = 0.68 at left parietal sites, and LN CR vs UN CR p = 0.68 at left parietal sites). Neither unexpected novelty, nor unexpected recollection modulates the amplitude of the later component. Results for both the early and late intervals are summarized in the bar plots shown in Figure 10.

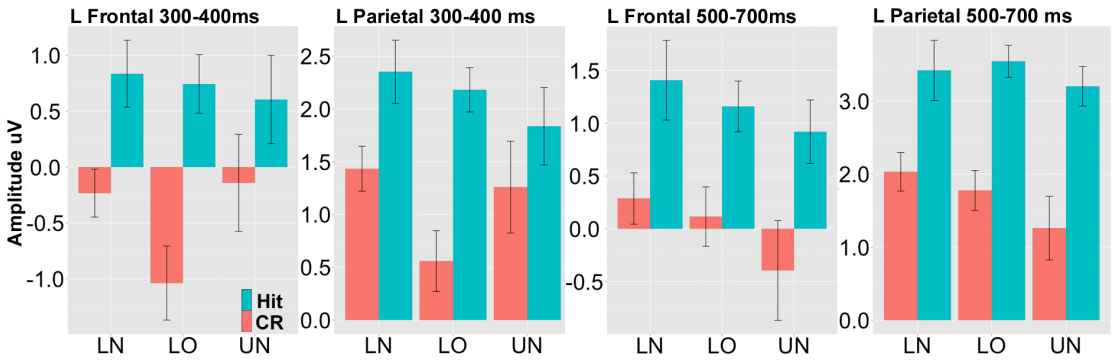

Figure 10: Barplots of mean amplitude at left frontal sites, 300-400ms after probe onset, left parietal sites, 300-400ms after probe onset, left frontal sites, 500-700ms after probe onset and left parietal sites, 500-700ms after probe onset.

Chapter 4: Discussion

The current study examined the effect of expectation on ERP indices of recognition memory. Prior fMRI findings (Jaeger et al., 2013; O'Connor et al., 2010) suggest the possibility that "retrieval success" effects seen in ERP experiments may not purely index recollection, but also other processes related to the recognition task, including those that evaluate the match between memory expectations and the contents of memory. Because of the low temporal precision of fMRI, these prior studies were not able to determine when expectancy effects occurred relative to functional correlates of memory processing. By employing ERPs, we were able to show two components tracking retrieval success, and that the earlier of these two components (300-400ms after probe onset at left parietal and frontal scalp regions) was sensitive to the match between cued expectations and memory content. Namely, when individuals were cued about the probable memory status of the probe and the cue and probe status were not congruent, early retrieval success effects were larger than when cues were congruent or neutral. This effect was primarily driven by more negative potentials for trials with a new probe falsely cued "likely old." Importantly, this component was evident before the onset of the typical late left parietal retrieval success component, which has been previously linked to recollective processing (Rugg & Curran, 2007; Vilberg et al., 2006).

The earlier time range, from 300-400ms after memory probe onset, has also previously been associated with a rapid familiarity-based recognition process (Curran, 2000; Curran, Tepe, & Piatt, 2006; Mecklinger, 2006; Rugg & Curran, 2007). By contrast, the later 500-700ms component was sensitive only to the status of probes in memory, and was not modulated by cues. Regardless of the cue type or cue-probe

correspondence, old items elicited a more positive going waveform relative to new items, which aligns with previous research associating this interval with recollection.

4.1 Electrophysiological response elicited by cueing

Examining ERPs elicited by cues revealed significant differences between cue types in the windows of 300-400ms and 700-850ms post cue onset. Further analysis indicated that individual differences in the overall memory decision criterion predicted amplitude for the later, but not the earlier component. The earlier component has a central scalp distribution, and is similar in topography and latency to the N400 component (Kutas & Federmeier, 2011). Previous research has indicated that less frequent stimuli and stimuli that are semantically ambiguous or incongruent modulate the amplitude of this component (Kutas & Federmeier, 2011; Laszlo & Federmeier, 2009). In the present study, amplitudes for this component were more negative for neutral cues relative to "likely old" or "likely new" cues, and this effect was more pronounced for strict responders, although group differences were not significant. This could reflect either the low frequency of neutral cues, which are 50% less frequent than either "likely old" or "likely new" cues, or may reflect the fact that neutral cues are ambiguous by nature. In contrast, during the time range of 700-850ms, strict responders, but not lax responders, showed significant amplitude differences by cue type. For strict responders, "likely old" cues elicited significantly greater amplitude signals than "likely new" or neutral cues. We are not aware of any similar anticipatory component identified in a recognition memory task, but cued anticipation has been associated with somewhat similar components in other tasks. For instance, cues indicating to prepare for an upcoming visual stimulus often elicit a more central, negative going slow potential called the contingent negative variation (CNV) (Bender, Resch, Weisbrod, & Oelkers-Ax, 2004; Brunia & van Boxtel,

2001). This potential, however, is associated with generic anticipation of a stimulus, while the correlation of the later component we observed with response bias suggests a process beyond anticipation alone. Since amplitude for the later component for strict responders was more positive for "likely old" cues and more negative for "likely new" cues, this might suggest it tracks anticipatory shifts in the decision criterion. However, the correlation of amplitude for this component with the behavioral measure of bias does not fully support this notion. The fact that amplitude differences in the responses to "likely old" and "likely new" cues in this range are both correlated with response bias on neutral trials suggests that these ERP components track overall shifts in cognitive set in "strict" individuals, rather than condition-specific shifts in response bias. Thus it is unclear from the current data what cognitive processes underlie these components, but the current data suggests anticipatory processing that is related to, but does not precisely index biasing of recognition memory.

4.2 Electrophysiological response elicited by memory probes

The current study revealed that the effect of expectancy on the retrieval success ERP response is temporally specific. The earlier component (300-400ms) was sensitive to violations of memory expectation, as revealed by an interaction between cueing and memory status while the later component (500-700ms) was not. The interpretation of these effects supports the view that some so-called "retrieval success" effects may index processes other than (or in addition to) the retrieval of episodic content, which may include processes related to the monitoring of the congruence between items recognized as old or new and their expected status in memory.

The temporal window that revealed an expectation-sensitive component was 300-400ms after presentation of probes, and this effect was particularly prominent at left

parietal and frontal electrode sites. There are a number of possible explanations for the greater "retrieval success" effect observed under invalid cueing during this time range, particularly the greater negativity seen for "likely old" correct rejections.

Although left parietal old-new effects have been previously associated with recollection, it seems unlikely that the recall of episodic content contributes to the earlier component. Retrieval success effects previously found in ERPs have typically showed a later onset, after 400ms (Friedman & Johnson, 2000; Rugg & Allan, 1995; Rugg & Curran, 2007), but it may be possible that the addition of explicit cues in the current task accelerates this component; trials where subjects are oriented to old items may elicit an earlier recollection effect than trials where subjects are oriented to new items. However, this would suggest that "likely old" hits and "likely new" hits would show amplitude differences in this time range, but amplitude was not significantly different for hits regardless of cue type – amplitude differences by cue type were only evident for correct rejections. This proposition does not fit well within most existing theoretical frameworks of memory retrieval, so we assume that recollection does not account for differences observed in the earlier time range.

The earlier component does differentiate hits and correct rejections under some conditions, and because the underlying memory process is not likely based on recollection, the earlier effect must be based on a distinct process. The time range from 300-400ms after the presentation of a memory probe has previously been associated with a retrieval success effect with a frontal scalp distribution, termed the FN400 (Curran, 2000; Curran et al., 2006; Mecklinger, 2006; Rugg & Curran, 2007). The FN400 is elicited by items correctly identified as old even when subjects fail to report having source memory for those items, suggesting that the underlying cognitive process is based on familiarity, rather than recollection. This recognition process is thought to be rapid,

automatic and devoid of contextual detail from encoding. Some authors propose that familiarity processes signal the strength of the global match between probe stimuli and the contents of memory (Hintzman, 1988), and others propose that it reflects the greater perceptual fluency afforded to repeated items, or a combination of the two (Jacoby, 1991; Yonelinas, 2002).

The 300-400ms component we observed seems consistent with these prior findings, but an additional process related to mnemonic expectation also modulates this component. Significant old-new effects were found in this range for trials with "likely old" cues, but neutral cue trials did not show an old-new effect from 300-400ms. Amplitude for neutral cue trials was intermediate, approximately the average of invalidly cued hits and CRs. One possible explanation for the lack of an old-new effect is that the observed component only tracks familiarity, and familiarity-based recognition is inactive or delayed unless participants are oriented to familiarity. This would not be consistent with a body of previous work suggesting that familiarity is automatic and insensitive to context. An alternative explanation is that the observed effect is a composite component tracking the congruence between a participant's expectations and the outcome of a familiarity assesment. Ecker and colleagues (Ecker, Zimmer, & Groh-Bordin, 2007a; Ecker, Zimmer, Groh-Bordin, & Mecklinger, 2007b) attempted to demonstrate that familarity is insensitive to spatial contextual manipulations, and in an initial study, successfully showed that manipulating the background had no effect on the familiarity ERP elicited by a memory probe item in the foreground (but see Tsivilis, Otten, & Rugg, 2001 for a conflicting report). However, they noted that when participants were not properly oriented to the foreground item, the background sometimes elicited a familarity effect as well, but the ERP reflected the summation of the two signals. Therefore, in a subsequent study, they used explicit cues to orient participants to foreground items before

they were presented, and found a pattern strikingly similar to our results. When participants were properly oriented by explicit spatial cueing, amplitude differences between old and new items were evident, but when participants were uncued, old-new effects were diminished or absent. We propose that the “likely old” cues in the present study have a similar effect on the 300-400ms component. The lack of a retrieval success effect for neutral and "likely new" cues does not suggest that familiarity-based recognition is entirely absent or delayed under these cue conditions, but rather than the component reflects the combination of expectation and familiarity. "Likely old" cues elicit the greatest signal contrast, while "unknown" and "likely new" cues reflect mixed or weaker mnemonic expectancy, and thus elicit smaller signal differences.

The timecourse of this effect is noteworthy, since the only previous demonstration of an expectation-related ERP effect in a recognition task we are aware of comes from Herron and colleagues (Herron et al., 2003), who identified an expectation effect with onset 800ms after the presentation of a memory probe, using a block by block probability manipulation of mnemonic expectations, rather than explicit memory cueing. Their result suggests a cognitive process reconciling expectations with the outcome of retrieval at a very late stage. In contrast, the current results suggest that mnemonic expectations interact with retrieval processing at a much earlier stage, before, rather than after the onset of classic recollection effects.

Critically, the temporal and topographic pattern of results seen from 300-400ms after the presentation of an invalidly cued novel item supports previous work noting heterogeneity among parietal processes supporting memory. Using fMRI, Jaeger and colleagues (Jaeger et al., 2013) recently demonstrated that multiple brain regions including the medial superior parietal lobule and regions of lateral PPC show a selective pattern of activation for unexpected new items using the same task. Some of these

regions neighbor or overlap regions previously associated with familiarity effects in neuroimaging, such as the intraparietal sulcus and precuneus (Henson et al., 2005; Montaldi et al., 2006; Vilberg & Rugg, 2007). If we assume both sets of regions are likely generators of the ERP seen from 300-400ms in our task, this would explain the broad topographic distribution of the expectation effect, and the variation in scalp topography between cue conditions seen in Figure 7. We propose that some of these regions track congruence between actual and expected familiarity strength for an item. Some regions of parietal cortex may support memory in a way that does not directly depend on successful retrieval of the encoding episode – rather these regions are involved in memory processing at an early stage that precedes recollection.

The later memory component (500-700ms) displayed a typical retrieval success effect that was not significantly affected by the correspondence between cue and memory probe. The latency and topography of this component matches previously identified recollection components (Friedman & Johnson, 2000; Vilberg et al., 2006) The preservation of a left parietal retrieval success effect from 500-700ms even in the face of invalid cues bolsters previous research indicating that this component tracks the recall of episodic content, independent of other processes supporting memory retrieval. All cue conditions showed retrieval success effects in this interval, with similar topography and onset. This also aligns with similar left parietal retrieval success effects which have been shown to be insensitive to similar expectation manipulations such as the relative probability of old and new items (Herron et al., 2003).

With the current study we have shown that directly manipulating mnemonic expectations via explicit cueing influences ERP indices of memory processing. Cues that indicate if upcoming probes are “likely old” or “likely new” elicit anticipatory processing that modulates the early stages of recognition. Memory probes are rapidly assessed first

via familiarity-based processing, with interactions between expectation and memory evident by 300ms after the presentation of a memory probe, well before the onset of recollection effects, around 500ms. When unexpected novelty (a "likely old" cue followed by a new item) is encountered, a greater negativity was seen in the ERP, while unexpected and expected familiar items elicited similar amplitude signals. This suggests that this component tracks not only the familiarity of an item, but the outcome of a rapid initial familiarity assessment in light of current expectations about an item. These findings align with a body of work indicating functional heterogeneity among parietal cortex during memory retrieval, and further suggests that these functional roles may be dissociated not only anatomically, but also temporally – parietal regions which are sensitive to expectation may be active earlier during a retrieval attempt than those which track recollection.

References

Aminoff, E. M., Clewett, D., Freeman, S., Frithsen, A., Tipper, C., Johnson, A., et al. (2012). Individual differences in shifting decision criterion: A recognition memory study. *Memory and Cognition*, *40*(7), 1016–1030. doi:10.3758/s13421-012-0204-6

Bender, S., Resch, F., Weisbrod, M., & Oelkers-Ax, R. (2004). Specific task anticipation versus unspecific orienting reaction during early contingent negative variation. *Clinical Neurophysiology*, *115*(8), 1836–1845. doi:10.1016/j.clinph.2004.03.023

Bergström, Z. M., Henson, R. N., Taylor, J. R., & Simons, J. S. (2013). Multimodal imaging reveals the spatiotemporal dynamics of recollection. *NeuroImage*, (68), 141–153. doi:10.1016/j.neuroimage.2012.11.030

Berryhill, M. E., Drowos, D. B., & Olson, I. R. (2009). Bilateral parietal cortex damage does not impair associative memory for paired stimuli. *Cognitive Neuropsychology*, *26*(7), 606–619. doi:10.1080/02643290903534150

Brunia, C., & van Boxtel, G. (2001). Wait and see. *International Journal of Psychophysiology*, *43*, 59–75. doi:10.1016/S0167-8760(01)00179-9

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nature Reviews Neuroscience*, *9*(8), 613–625. doi:10.1038/nrn2459

Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, *46*(7), 1828–1851. doi:10.1016/j.neuropsychologia.2008.03.022

Ciaramelli, E., Grady, C., Levine, B., Ween, J., & Moscovitch, M. (2010). Top-Down and Bottom-Up Attention to Memory Are Dissociated in Posterior Parietal Cortex: Neuroimaging and Neuropsychological Evidence. *The Journal of Neuroscience*, *301*(14), 4943–4956. doi:10.1523/JNEUROSCI.1209-09.2010

Coulson, S., King, J. W., & Kutas, M. (1998). Expect the Unexpected: Event-related Brain Response to Morphosyntactic Violations. *Language and Cognitive Processes*, *13*(1), 21–58.

Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory and Cognition*, *28*(6), 923–938.

Curran, T., Tepe, K., & Piatt, C. (2006). Event-related potential explorations of dual processes in recognition memory. In H. D. Zimmer, A. Mecklinger, & U. Lindberger (Eds.), *Binding in Human Memory: A Neurocognitive Approach* (pp. 467–492). Oxford: Oxford University Press.

Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2006). Triple Dissociation in the Medial Temporal Lobes: Recollection, Familiarity, and Novelty. *Journal of Neurophysiology*.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Neuropsychologia*, *134*(1), 9–21. doi:10.1016/j.jneumeth.2003.10.009

Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation

and success: separable neurocognitive components underlying episodic recognition. *Neuropsychologia*, *41*(3), 318–333. doi:10.1016/S0028-3932(02)00164-1

Düzel, E., Yonelinas, A. P., Mangun, G. R., Heinze, H.-J., & Tulving, E. (1997). Event-related brain potential correlates of two states of conscious awareness□in□memory. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(11), 5973.

Ecker, U. K. H., Zimmer, H. D., & Groh-Bordin, C. (2007a). Color and context: An ERP study on intrinsic and extrinsic feature binding in episodic memory. *Memory and Cognition*, *35*(6), 1483–1501. doi:10.3758/BF03193618

Ecker, U., Zimmer, H., Groh-Bordin, C., & Mecklinger, A. (2007b). Context effects on familiarity are familiarity effects of context — An electrophysiological study. *International Journal of Psychophysiology*, *64*, 146–156. doi:10.1016/j.ijpsycho.2007.01.005

Friedman, D., & Johnson, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique*, *51*(1), 6–28. doi:10.1002/1097-0029(20001001)51:1<6::AID-JEMT2>3.0.CO;2-R

He, P., Wilson, G., & Russell, C. (2004). Removal of ocular artifacts from electro-encephalogram by adaptive filtering. *Medical & Biological Engineering & Computing*, *42*, 407–412.

Henson, R. N., Hornberger, M., & Rugg, M. D. (2005). Further Dissociating the Processes Involved in Recognition Memory: An fMRI Study. *Journal of Cognitive Neuroscience*, *17*(7), 1058–1073. doi:10.1162/0898929054475208

Herron, J. E., Quayle, A. H., & Rugg, M. D. (2003). Probability effects on event-related potential correlates of recognition memory. *Cognitive Brain Research*, *16*(1), 66–73. doi:10.1016/S0926-6410(02)00220-3

Hintzman, D. L. (1988). Judgements of Frequency and Recognition Memory in a Multiple-Trace Memory Model. *Psychological Review*, *95*(4), 528–551.

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, *30*(5), 513–541. doi:10.1016/0749-596X(91)90025-F

Jaeger, A., Konkel, A., & Dobbins, I. G. (2013). Unexpected novelty and familiarity orienting responses in lateral parietal cortex during recognition judgment. *Neuropsychologia*, *51*(6), 1061–1076. doi:10.1016/j.neuropsychologia.2013.02.018

Johnson, J. D., & Rugg, M. D. (2007). Recollection and the Reinstatement of Encoding-Related Cortical Activity. *Cerebral Cortex*, *17*(11), 2507–2515. doi:10.1093/cercor/bhl156

Kutas, M., & Federmeier, K. D. (2011). Thirty Years and Counting: Finding Meaning in the N400 Component of the Event-Related Brain Potential (ERP). *Annual Reviews of Psychology*, *62*, 621–647. doi:10.1146/annurev.psych.093008.131123

Laszlo, S., & Federmeier, K. D. (2009). A beautiful day in the neighborhood: An event-related potential study of lexical relationships and prediction in context. *Journal of Memory and Language*, *61*(3), 326–338. doi:10.1016/j.jml.2009.06.004

Mecklinger, A. (2006). Electrophysiological Measures of Familiarity Memory. *Clinical*

EEG and Neuroscience, *37*(4), 292–299. doi:10.1177/155005940603700406
Montaldi, D., Spencer, T. J., Roberts, N., & Mayes, A. R. (2006). The neural system that mediates familiarity memory. *Hippocampus*, *16*(5), 504–520. doi:10.1002/hipo.20178
Neville, H. J., Kutas, M., Chensney, G., & Schmidt, A. L. (1986). Event-Related Brain Potentials During Initial Encoding and Recognition Memory of Congruous and Incongruous Words. *Journal of Memory and Language*, *25*, 75–92.
O'Connor, A. R., Han, S., & Dobbins, I. G. (2010). The inferior parietal lobule and recognition memory: Expectancy violation or successful retrieval? *The Journal of Neuroscience*, *30*(8), 2924. doi:10.1523/JNEUROSCI.4225-09.2010
Osterhout, L., & Holcomb, P. J. (1992). Event-Related Brain Potentials Elicited by Syntactic Anomaly. *Journal of Memory and Language*, *31*, 785–806. doi:10.1037/0278-7393.20.4.786
Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148. doi:10.1016/j.clinph.2007.04.019
Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the Detection of Signals. *Journal of Experimental Psychology: General*, *109*(2), 160–174. doi:10.1037/0096-3445.109.2.160
Rugg, M. D., & Allan, K. (1995). Event-Related Potential Studies of Memory. In *Memory Handbook* (pp. 521–537). Memory Handbook.
Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, *11*(6), 251–257. doi:10.1016/j.tics.2007.04.004
Rugg, M. D., Otten, L. J., & Henson, R. N. A. (2002). The neural basis of episodic memory: evidence from functional neuroimaging. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1424), 1097–1110. doi:10.1098/rstb.2002.1102
Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. A., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*, *46*, 1185–1191. doi:10.1016/j.neuropsychologia.2007.07.024
Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation Between Memory Accuracy and Memory Confidence Following Bilateral Parietal Lesions. *Cerebral Cortex*, *20*(2), 479–485. doi:10.1093/cercor/bhp116
Soltani, M., & Knight, R. T. (2000). Neural Origins of the P300. *Critical Reviews in Neurobiology*, *14*(3-4), 199–224.
Spaniol, J., Davidson, P. S. R., Kim, A. S. N., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation likelihood estimation. *Neuropsychologia*, *47*(8-9), 1765–1779. doi:10.1016/j.neuropsychologia.2009.02.028
Spencer, K. M., Abad, E. V., & Donchin, E. (2000). On the search for the neurophysiological manifestation of recollective experience. *Psychophysiology*, *37*(04), 494–506.
Tsivilis, D., Otten, L. J., & Rugg, M. D. (2001). Context Effects on the Neural Correlates

of Recognition Memory. *Neuron*, *31*(3), 497–505. doi:10.1016/S0896-6273(01)00376-2
Vilberg, K. L., & Rugg, M. D. (2007). Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia*, *45*(10), 2216–2225. doi:10.1016/j.neuropsychologia.2007.02.027
Vilberg, K. L., & Rugg, M. D. (2009). Left parietal cortex is modulated by amount of recollected verbal information. *Neuroreport*, *20*(14), 1295–1299. doi:10.1097/WNR.0b013e3283306798
Vilberg, K. L., Moosavi, R. F., & Rugg, M. D. (2006). The relationship between electrophysiological correlates of recollection and amount of information retrieved, *1122*(1), 161–170. doi:10.1016/j.brainres.2006.09.023
Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*(9), 445–453. doi:10.1016/j.tics.2005.07.001
Wheeler, M. E., & Buckner, R. L. (2003). Functional Dissociation among Components of Remembering: Control, Perceived Oldness, and Content. *The Journal of Neuroscience*, *23*(9), 3869–3880.
Yonelinas, A. P. (2002). The Nature of Recollection and Familiarity: A Review of 30 Years of Research. *Journal of Memory and Language*, *46*(3), 441–517. doi:10.1006/jmla.2002.2864
Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the Brain Regions Involved in Recollection and Familiarity in Recognition Memory. *The Journal of Neuroscience*, *25*(11), 3002–3008.
Yu, S. S., Johnson, J. D., & Rugg, M. D. (2012). Dissociation of recollection-related neural activity in ventral lateral parietal cortex. *Cognitive Neuroscience*, *3*(3-4), 142–149. doi:10.1080/17588928.2012.669363